Animal Behaviour

The reliability of individual vocal signature varies across the bonobos' graded repertoire

--Manuscript Draft--

Manuscript Number:	ANBEH-D-20-00122R2
Article Type:	UK Research paper
Keywords:	acoustic grading; Bonobo; identity information; individual vocal signature
Corresponding Author:	Florence Levrero Université Jean Monnet Saint-Etienne Saint-Etienne, FRANCE
First Author:	Sumir Keenan
Order of Authors:	Sumir Keenan
	Nicolas Mathevon
	Jeroen MG Stevens
	Florence Nicolè
	Klaus Zuberbühler
	Jean-Pascal Guéry
	Florence Levrero
Abstract:	Animal vocalisations often contain both 'dynamic' information, related to short-term fluctuations in the emitter's emotional states, and 'static' information, related to long-term attributes such as age, sex, weight and body size which define the emitter's "individual vocal signature". While both types of information may be of functional value to receivers, dynamic information requires acoustic versatility, while static information depends on acoustic stability. Here we investigate whether an individual vocal signature is present across the vocal repertoire of the bonobo, Pan paniscus . We first emphasize the graded character of the bonobo's repertoire by describing the acoustic structure of its five most common tonal vocalisations. We then evaluate the reliability of identity information across these call types. The results show that, while all call types support information related to the emitter's identity, the reliability of these vocal signatures was not consistent along the graded vocal continuum. Caller identity is strongly encoded at one end of the acoustic gradation (high-hoot) and decreases from bark, soft bark, peep-yelp to peep calls. Strikingly, the reliability of the individual signature thus decreases from calls used in high-arousal contexts to low-arousal contexts. To the best of our knowledge, this is the first demonstration that an acoustic gradation that codes for 'dynamic' information can be accompanied by variation of the 'static' information that supports vocal individuality.

The reliability of individual vocal signature varies across the bonobos' graded repertoire

Sumir Keenan[1,2], Nicolas Mathevon[1], Jeroen MG Stevens[3], Florence Nicolè[4], Klaus Zuberbühler[2,5], Jean-Pascal Guéry[6] and Florence Levréro[1]

[1]University of Lyon / Saint-Etienne, Equipe Neuro-Ethologie Sensorielle, ENES / CRNL, CNRS, INSERM, Saint-Etienne, 42100, France

[2]University of St. Andrews, Department of Psychology & Neuroscience, St. Andrews, Scotland, KY16 9JP, UK

[3]APELAB - Behavioural Ecology and Ecophysiology Group, Department of Biology, University of Antwerp, Belgium

[4]University of Lyon / Saint-Etienne, BVPam Lab, CNRS FRE 3727, Saint-Etienne, 42100, France

[5]Université de Neuchâtel, Department of Comparative Cognition, Neuchâtel, 2000, Switzerland

[6]Vallée des Singes Zoological Park, Romagne, 86700, France

Corresponding authors:

Sumir Keenan sumirkeenan@gmail.com

Florence Levréro florence.levrero@univ-st-etienne.fr

Highlights

- We investigated the coding of individual signature in a graded vocal repertoire.
- We compared the strength of individual vocal signature across the bonobo repertoire.
- Quantitative analysis revealed graded structure between most common call types.
- All call types investigated showed significant individual vocal signatures.
- The individual signature was stronger at one extreme of the vocal gradation.

The reliability of individual vocal signature varies across the bonobos' graded repertoire

Sumir Keenan[1,2], Nicolas Mathevon[1], Jeroen MG Stevens[3], Florence Nicolè[4], Klaus Zuberbühler[2,5], Jean-Pascal Guéry[6] and Florence Levréro[1]

[1]University of Lyon / Saint-Etienne, Equipe Neuro-Ethologie Sensorielle, ENES / CRNL, CNRS, INSERM, Saint-Etienne, 42100, France

[2]University of St. Andrews, Department of Psychology & Neuroscience, St. Andrews, Scotland, KY16 9JP, UK

[3]APELAB - Behavioural Ecology and Ecophysiology Group, Department of Biology, University of Antwerp, Belgium

[4]University of Lyon / Saint-Etienne, BVPam Lab, CNRS FRE 3727, Saint-Etienne, 42100, France

[5]Université de Neuchâtel, Department of Comparative Cognition, Neuchâtel, 2000, Switzerland

[6]Vallée des Singes Zoological Park, Romagne, 86700, France

Corresponding authors:

Sumir Keenan sumirkeenan@gmail.com

Florence Levréro florence.levrero@univ-st-etienne.fr

Highlights

- Coding of individual signature in a graded vocal repertoire
- Comparison of the strength of individual vocal signature across bonobo repertoire.
- Quantitative analysis revealed a graded structure between the most common bonobo call types.
- All call types investigated show significant individual vocal signatures.
- The individual signature is stronger in one extreme of the vocal gradation.

Abstract

Animal vocalisations often contain both ‘dynamic’ information, related to short-term fluctuations in the emitter’s emotional states, and ‘static’ information, related to long-term attributes such as age, sex, weight and body size which define the emitter’s “individual vocal signature”. While both types of information may be of functional value to receivers, dynamic information requires acoustic versatility, while static information depends on acoustic stability. Here we investigate whether an individual vocal signature is present across the vocal repertoire of the bonobo, *Pan paniscus*. We first emphasize the graded character of the bonobo’s repertoire by describing the acoustic structure of its five most common tonal vocalisations. We then evaluate the reliability of identity information across these call types. The results show that, while all call types support information related to the emitter’s identity, the reliability of these vocal signatures was not consistent along the graded vocal continuum. Caller identity is strongly encoded at one end of the acoustic gradation (high-hoot) and decreases from bark, soft bark, peep-yelp to peep calls. Strikingly, the reliability of the individual signature thus decreases from calls used in high-arousal contexts to low-arousal contexts. To the best of our knowledge, this is the first demonstration that an acoustic gradation that codes for ‘dynamic’ information can be accompanied by variation of the ‘static’ information that supports vocal individuality.

Keywords: acoustic grading; bonobo; identity information; individual vocal signature

INTRODUCTION

Bird and mammal vocalisations usually contain both ‘dynamic’ information, related to short-term fluctuations in the emitter’s physiological and psychological states, and ‘static’ information, related to idiosyncratic features such as age, sex, weight, and body size which define the emitter’s “individual vocal signature” (Briefer, 2012, 2020; Charlton, Pisanski, Raine & Reby, 2020; Pisanski, Nowak, & Sorokowski, 2016; Raine, Pisanski & Reby, 2017; Taylor, Charlton & Reby, 2016). Both dynamic and static information likely have important roles in a wide range of social contexts (Taylor, Charlton & Reby, 2016). The acoustic coding of dynamic information relies on versatile acoustic features that can be modulated depending on the emitter’s current internal state (Briefer 2012, 2020; Pisanski, et al., 2016a; Raine, Pisanski & Reby, 2017; Taylor, Charlton & Reby, 2016), and can be reflected in a repertoire of discreet call types (Bradbury & Vehrencamp, 1998; Cheney & Seyfarth, 2018; Maynard-Smith & Harper, 2003;), and/or in more subtle acoustic variations within each call type (graded vocalisations; Briefer, 2012, 2020). Sometimes, the acoustic boundaries between call types are unclear that the whole vocal repertoire can be considered as a graded system (e.g. Fischer, Wadewitz & Hammerschmidt, 2017; Hammerschmidt & Fischer 1998; Keenan, Lemasson & Zuberbühler, 2013; Manser et al., 2014; Marler 1977; Tallet et al., 2013). While dynamic information requires acoustic versatility, static information defining an “individual vocal signature” should depend on acoustic stability. How do animal signals deal with this potential conflict of information coding?

One solution is temporal segregation, which has been demonstrated in the vocalisations of the banded mongoose (*Mungos mungo*). This species produces calls containing two successive distinct segments, the first being stable and individually distinct, and the second being graded and correlating with the emitter's current behaviour (Jansen, Cant & Manser, 2012). Whether temporal segregation is a rare or a widespread way of separately coding dynamic and static information in vocal signals is a question that remains to be answered.

Another solution would be to keep the indexical acoustic cues supporting individual signatures stable across the whole vocal repertoire. This would mean a common set of individualized acoustic features, either shared between calls when the repertoire is composed by discreet calls or remaining invariable throughout a graded repertoire. Unfortunately, this hypothesis has been barely tested, as the vast majority of studies investigating individual vocal signatures have only focused on a single vocalisation type (e.g. in birds: blue footed boobies, *Sula nebouxii*, Dentressangle, Aubin & Mathevon, 2012; jungle crows, *Corvus macrorhynchos*, Kondo, Izawa & Watanabe, 2010; multiple species of penguins, Aubin & Jouventin 2002 ; in mammals: bats, *Saccopteryx bilineata* and *Noctilio albiventris*, Knörnschild & Von Helversen 2008; Voigt-Heucke, Taborsky & Dechmann, 2010; elephants, *Loxodonta africana*, Soltis, Leong & Savage, 2005; hyenas, *Crocuta crocuta*, Mathevon, Koralek, Weldele, Glickman & Theunissen, 2010; marmots, *Marmotta sp.*, Matrosova, Blumstein, Volodin & Volodina, 2011; seals, *Arctocephalus tropicalis*, Charrier, Mathevon & Jouventin, 2003; northern elephant seals, *Mirounga angustirostris,* Casey,

Charrier, Mathevon & Reichmuth, 2015; chimpanzees, *Pan troglodytes schweinfurthii*, Levréro & Mathevon 2013, and spider monkeys, *Ateles geoffroyi*, Chapman & Weary 1990). To the best of our knowledge, there has only been one study that has examined the coding of individual signature throughout a whole repertoire composed by discreet calls, in the zebra finch *Taeniopygia guttata* (Elie & Theunissen, 2018). In this songbird, individual recognition is of primary importance for pair bonding (Vignal, Mathevon & Mottin, 2004). Elie & Theunissen (2018) showed that each zebra finch call type displays a distinct individual signature, and, contrary to expectations, there is no common set of static, individualized, acoustic features. Instead, the vocal repertoire of a given emitter supports numerous signatures, and receivers have to memorize all of them to perform individual recognition. Moreover, the Elie & Theunissen (2018) zebra finch study, as well as the few other studies that have analysed more than one call type within a species' vocal repertoire, have emphasised that the reliability of individual signatures may vary among calls (e.g. putty-nosed monkeys, *Cercopithecus nictitans,* Price, Arnold, Zuberbuhler & Semple 2009; fallow deer, *Dama dama,* Vannoni & McElligott 2007, but see western gorilla, *Gorilla gorilla,* Salmi, Hammerschmidt & Doran-Sheehy, 2014). For instance, Charrier, Jouventin, Mathevon & Aubin (2001) found that both courtship and contact calls of a marine bird, the South Polar Skua (*Catharacta maccormicki*), have a higher potentiality of individual identity coding than the alarm call. In the red-capped mangabey (*Cercocebus torquatus*), a monkey living in the African rainforest, individual distinctiveness is higher in contact and threat calls than in

other vocalisations (Bouchet, Blois-Heulin, Pellier, Zuberbuhler & Lemasson, 2012). Recently, Rubow, Cherry & Sharpe (2017) found similar results among the repertoire of the dwarf mongoose (*Helogale parvula*).

While a proximal explanation for signature inconstancy within a repertoire likely depends on variations in the shape of the vocal tract accompanying modulation of acoustic production (review in Charlton, Pisanski, Raine & Reby, 2020), its functional value remains uncertain. Although it may have no specific functional consequences (e.g. Rendall, Owren & Rodman, 1998), alternative hypotheses state that individual signatures differ across call types as an adaptive response to various socio-ecological pressures. On one hand, the 'distance communication hypothesis' predicts that in low visibility environments, such as dense forests, natural selection will favour individual signatures in vocal signals used to communicate over long distances beyond the visible range (Ey & Fischer 2009; Mitani & Stuht 1998). This hypothesis has received some support by comparing two chimpanzees' vocalisations, a long distance and a short-range call (Mitani, Gros-Louis & Macedonia, 1996). On the other hand, the 'social function hypothesis' (Price, Arnold, Zuberbuhler & Semple, 2009; Snowdon & Hausberger, 1997) predicts that the reliability of individual vocal signatures depends on the social role of a call type. If the vocalisation is emitted in a context where being recognized is of primary importance for individual-specific relationships, such as mated pair bonds, mother-young bond, or tolerant relationships between neighbours in territorial animals, it should bear reliable information about individual identity (Kondo & Watanabe, 2009; Kreiman &

156 Sidtis, 2011; Wiley, 2013). This hypothesis has been supported in birds
157 (Charrier, Jouventin, Mathevon & Aubin, 2001; Elie & Theunissen, 2018) and
158 some non-human primate species (e.g. mouse lemurs, *Microcebus murinus*
159 (Leliveld, Scheumann & Zimmermann, 2011), Campbell's
160 monkeys, *Cercopithecus campbelli campbelli* (Lemasson & Hausberger, 2011).
161 However, these distant-communication and social function hypotheses may not
162 be mutually exclusive. For instance, distance calls can play a significant role in
163 social regulation, facilitating cooperation, such as the recruitment of
164 conspecifics for support (Gersick, Cheney, Schneider, Seyfarth, & Holekamp,
165 2015; Mitani & Nishida, 1993), coordinating travel (Schamberg, Cheney, Clay,
166 Hohmann & Seyfarth, 2016), signalling food ownership (Gros-Louis 2004;
167 Heinrich & Marzluff, 1991), or conveying the aggressive or peaceful intentions
168 of callers (Searcy, Anderson & Nowicki, 2006; Silk 2002).

169 To explore how an animal vocal repertoire can deal with the potential conflict of
170 coding both dynamic information (e.g. expressing motivation,
171 aggressiveness…) and static information (i.e. a vocal signature supporting
172 individual recognition), here we investigate variations in the strength of vocal
173 individual signature throughout the graded vocal repertoire of an ape species,
174 the bonobo. Bonobos display a complex vocal repertoire with highly graded call
175 types used flexibly across contexts (Bermejo & Omedes, 1999; de Waal, 1998).
176 Despite growing interest in the acoustic communication of this species, our
177 current knowledge of the information content of bonobo calls is limited, as only
178 few studies have qualitatively described the bonobo vocal repertoire (Clay,

179 Archbold & Zuberbuhler, 2015; Clay & Zuberbuhler, 2009, 2011a, 2011b;
180 Keenan et al., 2016; White, Waller, Boose, Merrill & Wood, 2015).

181 Bonobo society is characterised by co-dominance between the sexes (Surbeck
182 & Hohmann, 2013) and complex fission-fusion dynamics which require
183 sophisticated social knowledge and communication (Clay, Archbold &
184 Zuberbuhler, 2015; Furuichi, 2011). It has been suggested that individual vocal
185 recognition is essential for successful social navigation (White, Waller, Boose,
186 Merrill & Wood, 2015). In a recent work (Keenan et al., 2016), we experimentally
187 demonstrated that bonobos can vocally identify familiar to unfamiliar individuals
188 using the peep-yelp, a soft vocalisation used in short range interactions. This
189 study already revealed that soft calls convey information about individual
190 signature, which is extracted by conspecifics. Other calls from bonobos'
191 repertoire are good candidates to convey individual signatures regarding their
192 propagation capacity in close habitat and their functions. Bonobos loud call
193 types, e.g. high-hoots, can be heard from a distance of 500 meters in the forest
194 (Hohmann & Fruth, 1994), and are regularly used by community members to
195 communicate with one another when the group splits into foraging parties
196 throughout the day. These vocalisations enable the sub-parties to convene
197 around a resource, such as a fruit-bearing tree or nesting tree, despite potential
198 distances between parties (Bermejo & Omedes, 1999; Hohmann & Fruth, 1994,
199 1995; Schamberg, Cheney, Clay, Hohmann & Seyfarth, 2016, 2017; White,
200 1996; White, Waller, Boose, Merrill & Wood, 2015). High-hoots are also
201 exchanged when different communities encounter one another, and they appear

to influence inter-community interactions (Furuchi, 2011; Hohmann & Fruth, 2002). Caller identity signalling may thus be present in the bonobos' calls with various acoustic structure and functions.

In this study, we test the hypothesis that an individual signature does exist across the graded vocal repertoire of the bonobo, but that the reliability of this signature varies along with the variation of the acoustic features defining the call types. We firstly emphasize the graded character of the bonobo's repertoire by providing a quantitative description of the acoustic structure of the five most common tonal call types, as well as their contextual use. We then compare the individual distinctiveness across call types.

METHODS

Ethics Statement:

All research conducted for this research paper was observational and no experimental manipulations occurred. All data collection protocols were performed in accordance with the relevant guidelines and regulations, and were approved by the Institutional Animal Ethical Committee of the University of Lyon/Saint-Etienne, under the authorization no. 42-218-0901-38 SV 09 (Lab ENES).

Subjects

The bonobos observed for this study were members of three separate captive groups housed at three European zoos: Apenheul (Apeldoorn, the Netherlands), Planckendael Zoo (Mechelen, Belgium) and la Vallée des Singes (Romagne, France; see Supplemental Table A1 for group composition at each zoo). At each zoo, groups were housed in large indoor enclosures with varying access to off-exhibit rooms and outdoor islands. All individuals included in the study had lived in similar captive zoo environments certified by the European Association of Zoos and Aquaria for a minimum of 10 years prior to recording. Vocal recordings and observations were taken from all areas at all three zoos, except in the off-exhibit enclosures at Apenheul.

To avoid the potential confound of differences in vocal tract size due to age, only bonobos over the age of 10 were included in this study. Additionally, one adult male and one female, who had overall low calling rates, were excluded. This led to a total of 21 individuals ranging in age from 10 – 45, with a mean age of 20.5 years old, and comprised of 13 females and 8 males.

Data Collection

Vocal recordings

Vocal recordings were collected between March 2013 and March 2014, beginning no earlier than 8 a.m. and finishing no later than 6 p.m. Recordings at Apenheul Zoo were collected from May 14, 2013 – July 6, 2013, as well as on March 12, 2014, and amounted to 175 hours of total recording time.

Recordings at Planckendael Zoo were collected from March 20, 2013 – May 10, 2013 and from February 20 – March 4, 2014, and amounted to 190 hours of total recording time. Recordings at la Vallée des Singes were collected from October 28, 2013 – November 25, 2013, and amounted to 115 hours of total recording time.

Audio recordings were taken using a Zoom H4 Digital Multi-track Recorder (44.1 kHz sample rate, 16 bits per sample, .wav files) - recording in stereo, with one channel devoted to a Sennheiser MKH70-1 ultra-directional microphone recording any bonobo vocal behaviour and the second channel connected to a micro-tie recording device, model AKG MPA III, for comments by the researcher. This allowed for temporal synchronising of each vocalisation to information on vocaliser identity and call context, as recorded by the researcher.

Call types

Each call was assigned to one of the 11 types based on classifications described in previous studies (Bermejo & Omedes, 1999; Clay & Zuberbuhler, 2009; de Waal, 1988) by SK. We calculated the frequency with which each call type was produce so that we could assign a proportion to each call type in the entire dataset (relative to the 2,373 measurable calls collected from the 21 adults included in the study). Any call type that represented less than 10% of the total number of measurable calls collected was excluded from the analysis. In addition, two call types, screams and grunts, were excluded from the current

study, due to their noisy acoustic features characterised by non-linear phenomena and lack of clear harmonic structure. Unlike the rest of the adult vocal repertoire, these two call types would require a different set of measurements to describe their acoustic features. In total, five call types were retained, which represented the vast majority of calls emitted by all individuals in the study groups (78% of all calls collected, excluding screams and grunts): (1) high-hoots (14%; described as 'staccato-high hoots' by de Waal (1988) and 'high hoots' by Bermejo & Omedes (1999)); (2) barks (18%; described as 'barks' and 'wieew barks' by de Waal (1988) and as 'barks' and 'composed barks' by Bermejo & Omedes (1999)); (3) soft barks (17%; described as 'soft barks' by Bermejo & Omedes (1999), 'food barks' by Clay & Zuberbuhler, (2009) and not described by de Waal (1988); (4) peep-yelps (18%; described as 'peep-yelps' by de Waal (1988); Bermejo & Omedes (1999); Clay & Zuberbuhler (2009) and (5) peeps (11%; described as 'peeps' by de Waal (1988); Bermejo & Omedes (1999); Clay & Zuberbuhler (2009); see Supplemental Table A2 for full acoustic description of each call type).

Call contexts

If a caller could be identified, social and individual contextual information was also recorded. Each recorded call occurred in one of the following eight contexts: 1) 'pre-feeding' – calls given directly prior to or at the start of scheduled feedings when group/social excitement was extremely high (excitement described as increased sexual activity, displacements, pacing, pilo-erection,

293 vocal activity, displays and increased likelihood of aggression); 2) ‘feeding’ –
294 calls given during scheduled feedings; 3) ‘foraging’ – calls given when foraging
295 for or eating food found outside or in the inside enclosure outside of scheduled
296 feeding times; 4) ‘aggression’ - calls given during agonistic encounters, including
297 mild aggression (no physical contact), aggression (mild physical contact, such
298 as hitting, kicking or grabbing between only two individuals), conflict (a range of
299 physical contact, including biting, and often between more than two individuals)
300 - agonistic interactions were also classified into calls from victims, from
301 aggressors or from bystanders; 5) grooming - calls given during bouts of
302 grooming; 6) contact – calls given when a subject was resting or moving but
303 nothing else; 7) change of environment – calls given when individuals were
304 shifted from one enclosure to another or from inside to outside; and 8) external
305 event – calls given when an individual was visibly startled by or responding to a
306 disturbance external to the group.
307
308 **Acoustic Analysis**
309
310 Only vocalisations that could unequivocally be assigned to one caller were
311 retained for analysis. Only calls of good, measurable quality were included,
312 while calls that overlapped with background noise (e.g. birds chirping, water
313 falling, zoo visitors speaking or other bonobos calling) were removed from the
314 dataset. In total, 1,850 individual calls were retained for analyses (with an
315 average of 88 total calls per individual (*N*=21), S.D.= 37.87, minimum=45,

maximum=227). Raven Pro 1.3 was used to measure automatic and manual parameters on each call and spectrograms were generated using a 512-sample Hann window (50% frame overlap, frequency resolution of 86.1 Hz and temporal resolution of 11.6 mS). A correlation matrix was produced and very highly correlated variables were removed (0.9 and above), resulting in a total of 16 measurements being retained for analysis – nine manually measured parameters describing the fundamental frequency and its temporal modulation, and seven automatically computed parameters describing the distribution of energy across the frequency spectrum of the entire call (Table 1; Figure 1).

Statistical Analysis

Call type distinctiveness

To confirm whether our dataset could be reliably classified into the five main call types proposed by previous studies, we performed a multivariate permuted discriminant function analysis (pDFA) to determine the statistical distinction between the 1,850 individual calls (high-hoots: *n*=333, barks: *n*=431, soft barks: *n*=413, peep-yelp: *n*=420, peeps: *n*=253; See Supplemental Table A2 for acoustic description of each call type). The raw values of the 16 acoustical parameters of interest were centred and normalised by transforming them into *z*-scores as the parameter set consisted of different units.

Mundry and Sommer (2007) have convincingly argued that using traditional discriminant function analyses (DFA), when analysing non-independent data (e.g. if the same individual contributed multiple calls), is a case of pseudo-replication and can inflate results. To address this issue, we employed a permuted discriminant function analysis (pDFA - Mathevon et al., 2010; Mundry & Sommer 2007) using the 16 acoustic variables (analysis performed in R, Version 3.2.0). The pDFA takes the classic DFA a step further by comparing the distribution of percent correct classifications obtained after 100 iterations (mean effect size) to the distribution of percent correct values obtained by initially randomly assigning the call type to each individual call (for the current analysis this distribution was obtained via 1000 created data sets where the call type of each call was randomly permutated).

In detail, we performed the following steps. In the first step of the DFA, a training data set was used to generate a set of linear discriminant functions. The training data set consisted of randomly selected sounds from each individual. The number of sounds selected per individual was the same for all individuals and equal to 2/3 of the smallest number of sounds that we obtained for an animal in our data set. In the second step, the discriminant functions generated from the training data set were used to classify the remaining sounds. For each individual, at least 1/3 of the sound provided by each individual was thus included in the validating data set. This cross-validation step gives a measure of the effect size (the percentage of correctly classified sounds; which has to be

362 compared with chance, here 20%, i.e. 1/5 possible call types). We ran 100
363 iterations of these two-step DFAs with both training and validation data sets
364 chosen at random. The mean effect size (mean percentage of correctly
365 classified sounds) was obtained by calculating the average of the percentages
366 of correctly classified sounds obtained with each of the 100 validation data sets.
367 In addition to the cross-validated DFAs performed on original data sets, new
368 data sets were also created, where the identity of sounds was randomly
369 permuted between individuals (permuted DFA), to obtain the statistical
370 significance of the mean effect size. From these randomised sets, the same
371 steps, fitting and validation, were consecutively performed. After 1000 iterations,
372 we calculated the proportion of randomized validation data sets revealing a
373 number of correctly classified calls being at least as large as the effect size
374 obtained with the non-randomised validation data set. This proportion gives the
375 significance of the discrimination level and is equivalent to a p-value
376 [Dentressangle, Aubin & Mathevon, 2012; Mathevon, Koralek, Weldele,
377 Glickman & Theunissen, 2010; Mundry & Sommer 2007].
378
379 *Individual vocal signatures*
380 We assessed the reliability of individual signatures for each call type
381 independently using two different approaches: the first approach used a pDFA
382 (same method as described above, except that calls within each call type were
383 classified according to the identity of the vocaliser; here the chance of correct
384 classification was 10%, i.e. 1/10 possible individual callers), and secondly by

385 calculating the acoustic variation and potential for individual coding (PIC) for
386 each call type overall, as well as for each acoustic parameter describing the
387 calls (Robisson, Aubin & Bremond, 1993).
388
389 The amount of variability across the five call types was determined by
390 calculating the inter- and intra-individual coefficients of variation (CV). Intra-
391 individual CVs correspond to the variability of each acoustic variable within
392 individuals, and inter-individual CVs correspond to the variability of each
393 acoustic variable between individuals (see mathematical formula below). The
394 CV values were then used to calculate potentials of individual coding (PICs) for
395 each acoustic variable in each call type (according to Robisson, Aubin &
396 Bremond, 1993). For each considered acoustic parameter, the PIC corresponds
397 to the ratio between the variability between individuals and the mean variability
398 within individuals. A PIC value greater than one suggests that the acoustic
399 parameter considered may be used for individual recognition as its intra-
400 individual variability is smaller than its interindividual variability. Additionally,
401 recent studies investigating individual distinctiveness in non-human primates
402 have calculated CV and PIC values, including them here enables direct
403 comparison between species (Bouchet, Blois-Heulin, Pellier, Zuberbuhler &
404 Lemasson, 2012; Lemasson & Hausberger, 2011; Salmi, Hammerschmidt &
405 Doran-Sheehy, 2014). As the coefficient of variation (CV) can only be calculated
406 with variables on a ratio scale, two variables (that were on an interval scale)
407 were not included (Slope– F_0 Start to Mid and Slope– F_0 Mid to End). Therefore,

for each of the remaining 14 parameters in each call type separately we first calculated the CV(Inter) = (100 X S.D. calculated across all individuals) / (Mean (calculated across all individuals)) and the CV(Intra) = the mean of individual CV values, where the CV (= 100 X S.D./Mean) was calculated for each individual separately. PIC values could then be obtained for each parameter (PIC = CV(Inter)/ CV (Intra)). To assess the variation of the five call types as a whole, we took the mean of the CV(Inter) and the CV(Intra) across the 14 parameters for each call type separately. These means were then used to calculate the PIC values for each call type. To test for call type differences in the levels of variation and potential for individual coding, Friedman tests were done with the CV and PIC values for each parameter for each call type respectively.

For the acoustic variation and PIC analyses, we included all individuals with 12-20 calls for each call type. For individuals who had more than 20 calls in a given call type, we randomly chose calls to be excluded (however ensuring where possible that a single calling event or calls given in a single day were not over-represented). This ensured that no single individual was overrepresented, as no individual contributed more than 20 calls for each call type.

For the pDFA analysis, we retained individuals who had a minimum of 14 calls for each call type (with the exception of one individual who had 13 calls in the peep call type) (See Supplemental Table A1 for the number of calls contributed by each individual for each call type). Not every individual had a sufficient

number of calls for each call type to be included in all five-call type analyses. The peep call-type had the fewest number of contributing individuals (*n*=10). To allow for direct comparison across call types, we randomly chose ten individuals for each of the other four call types (balancing the data for individual sex and group), with the majority of individuals contributing to 2 or 3 call type analyses (mean = 2.5, max = 4, min = 1; Supplemental Table A1).

We considered the identity of callers to assess the individual vocal signature, but not the sex, rank or age. Indeed, sex information is one of the many other elements that constitute individual identity. A receiver may identify the overall identity of a familiar caller and not need to categorize it by its sex. To identify other parameters and their interactions that may influence the identity signature was beyond the scope of this study.

RESULTS

Call types – Classification and context

The results of the pDFA showed that the acoustic structure of calls supports the initial, human-driven, classification into call types, with an accuracy of 57% (chance = 20%, $P < 0.001$; Figure 2).

A scatterplot using discriminant function 1 and 2 to visualise the grouping of the call types, fails to show any distinct boundaries between the five call types,

454 suggesting acoustic grading (Figure 3). We observed a crescent shape from the
455 soft peep to loud high-hoot, which highlights the strong graded nature of the
456 most common call types in the vocal system of the bonobo.
457
458 Despite the gradedness of the five call types, overall the call types were used
459 significantly differently from one another in different contexts ($\chi 2 = 930.281$, $P <$
460 0.001; results of Chi-square on contingency table of observed vs. expected
461 number of calls emitted in each context for each call type) (Table 2), and post-
462 hoc tests revealed that each call type was used significantly differently from
463 each other call type (see Supplemental Table A3 for details). The high-hoots
464 were used most often before feeding times (pre-feeding) and by aggressors in
465 agonistic encounters (aggression), but also during changes in environment and
466 to external events (or alarm). Barks were given in similar contexts to high-hoots,
467 however, with a marked increase of calls being given during feeding events. Soft
468 barks were given mostly in association with feeding and foraging, but also during
469 pre-feeding events. Peep-yelps and peeps, finally, were used similarly with the
470 main difference being an increased usage of peeps during grooming and contact
471 and a decreased usage during feeding or foraging (Table 2).
472
473 **Individual vocal signature**
474 Five separate pDFA analyses were run on each call type to evaluate the level
475 of individual distinctiveness along the graded repertoire. Calls were assigned to
476 the correct emitter 53% of the time for high-hoots (chance level = 10%; $P =$

0.001), 44% for barks (chance level = 10%; P = 0.001), 30% for soft barks (chance level = 10%; P = 0.001), 25% for peep-yelps (chance level = 10%; P = 0.004) and 23% for peeps (chance level = 10%; P = 0.006) (all percentages were from cross-validated data sets; Figures 3 and 4; Supplemental Tables A4, A5, A6, A7, A8).

Variability and vocal signature

All of the call types had PIC values over 1, indicating that all five have some capacity to code for individuality, however the PIC was significantly stronger in some call types (Friedman test of PIC values: χ^2 (13) = 49.114, P < 0.001). PIC was highest in high-hoots (1.22), followed by barks (1.18), peep-yelps (1.10), soft barks (1.08) and peeps (1.03) (Table 3).

We then used this information to investigate which of the acoustic parameters had the highest potential for individual coding. Across all call types the onset frequency of the fundamental frequency (F_0-Start) (1.20) and the ascending slope (1.22) had the highest PIC values (Table 3). However, when investigating each call type separately, these two parameters did not always have the highest potential for individual coding. The onset frequency of the fundamental frequency (F_0-Start) had the highest PIC in both the peep and barks, while the maximum frequency reached on the fundamental frequency (F_0-Peak) had the highest PIC in peep-yelps and high-hoots and the call duration and the frequency of the fundamental at the end of the call (F_0-End) equally had the

highest PIC for soft barks. Additionally, for each call type separately not all acoustic parameters reached the minimum threshold (PIC ≤ 1) of identity coding (Table 3). It is clear that acoustic parameters related to the tonality had consistently higher PIC values than the parameters describing the energy distribution for all five call types.

DISCUSSION

Our results demonstrate that the bonobo tonal calls investigated show clear individual vocal signatures. Furthermore, the results support our hypothesis that the reliability of this signature varies along the graded vocal continuum formed by these calls. Caller identity signalling is stronger at one end of the acoustic gradation (high-hoot) and then decreases from bark, soft bark, peep-yelp to peep calls. The reliability of the individual signature thus decreases from calls mostly used in high-arousal contexts to the ones used in low-arousal contexts. To the best of our knowledge, this is the first demonstration that the acoustic gradation that codes for ‘dynamic’ information can be accompanied by a gradation of the strength of the ‘static’ information that supports vocal individuality.

Individual signatures are the result of idiosyncratic acoustic features characterizing each individual. These features are constrained by the biomechanics of sound production, which varies depending on individual

morphology, anatomy, and physiology. As such, a proximal explanation for the variation of the strength of individual signature across the vocal repertoire is that the acoustic features of calls do not have the same potential for encoding individual variation. Soft calls, namely characterized by little to no frequency modulation and short durations, may offer reduced possibility for encoding identity cues. Conversely, highly frequency modulated calls as the high-hoot may support higher possibilities for individual differences.

Importantly, we recently demonstrated with playback experiments that bonobos are able to discriminate between the peep-yelps of familiar and unfamiliar individuals (Keenan et al., 2016). This suggests that even the call types with a less reliable individual signature may contain enough identity information for individual recognition in bonobos. Similar findings with various species have demonstrated that individuals are able to utilize acoustically encoded identity information to recognise others even in calls with low potential for individuality (e.g. in zebra finches – Elie & Theunissen, 2018; northern fur seals, *Callorhinus ursinus* – Insley, 2000; domestic horses*, Equus caballus* – Proops, McComb & Reby, 2009; and rhesus macaques *Macaca mulatta* – Rendell, Rodman & Emond, 1996). However, peep-yelps, and other soft calls, may greatly suffer from long range propagation through the forest environment. We assume that the individual signature carried by these calls should be efficient only at short-range. We suggest that the increase in signature reliability from peeps to high-hoots may be functionally relevant since it allows louder calls, which propagate

546 further, to maintain the fidelity of individual information (“distance hypothesis”,
547 Ey & Fischer, 2009; Fedurek, Zuberbühler & Dahl, 2016; Mitani, Gros-Louis &
548 Macedonia, 1996; Mitani & Stuht 1998). It is also possible that the social value
549 of individual recognition increases from peeps to high-hoots (“social function
550 hypothesis”, Price, Arnold, Zuberbuhler & Semple, 2009; Snowdon &
551 Hausberger, 1997; Snowdon & Hausberger 1997).
552
553 Whether variation in the reliability of individual signatures across a vocal
554 repertoire is an adaptive response to socio-ecological pressures is still debated.
555 Similar to our data, a recent study (Salmi, Hammerschmidt & Doran-Sheehy,
556 2014) investigating individual distinctiveness in both close and long range call
557 types of female western gorillas (*Gorilla gorilla gorilla*), found that all call types
558 had the same potential for individual coding. The authors concluded that neither
559 the social function nor the distance hypotheses accurately reflected the possible
560 evolutionary pressures likely acting on female gorilla calls.
561
562 While gorillas are the only other ape species where multiple call types were
563 investigated, Mitani et al. (1996) studied two call types in chimpanzees, the
564 bonobo’s congener. They found, as in our study, that loud calls contained
565 stronger identity information than soft calls used when in close contact with other
566 individuals. Chimpanzees and bonobos both live in dense rain forests, forming
567 far more complex fluid fission-fusion societies compared to the gorilla’s largely
568 stable polygynous group structure (Robbins, Bermejo, Cipolletta, Magliocca,

569 Parnell, & Stokes, 2004). This difference in social structure, and the need to
570 regularly communicate with group members over long distances, is likely a
571 driving evolutive pressure for accurate identity signaling over long distance.
572
573 So far acoustically graded calls have been overlooked in animal communication
574 research, despite being widespread in the vocal repertoire of terrestrial
575 mammals (Crockford, 2019; Fischer, Wadewitz & Hammerschmidt, 2017). This
576 lack of knowledge is mainly due to the complexity of capturing and describing
577 the variations in the signal repertoires without forcing arbitrary categorizations
578 (Fischer, Wadewitz & Hammerschmidt, 2017). Yet, a comparative perspective
579 on graded repertoires of non-human primates and other mammals may inform
580 understanding of our own vocal repertoire. Indeed, the non-verbal vocalisations
581 of humans (e.g. laughter, cries, and screams) resemble those of non-human
582 mammals, especially when one considers how they greatly fluctuate in their
583 acoustic structure (Briefer 2012, 2020; Morton, 1977). Despite their importance
584 in human social regulation, how individual vocal signatures change or are
585 preserved across calls used in a diversity of communication contexts -from joy
586 to distress- is also poorly known. A recent study in humans revealed that
587 individual differences in fundamental frequency (F0), which is an important
588 biosocial marker during speech production (for reviews Lavan, Burton, Scott &
589 McGettigan, 2019; Pisanski, Cartei, McGettigan, Raine & Reby, 2016), may be
590 preserved across non-verbal sounds (from laughter to screams) in largely
591 valence-specific manner. For instance, individual differences in F0 were

preserved across pain vocalisations representing varying levels of pain intensity (Pisanski, Raine & Reby, 2020). Pisanski et al. (2016b) argued that the high ability of humans to voice modulation is likely to predate our ability to articulate the verbal dimension of speech. Here we raise the question whether a vocally graded repertoire is to some extent a form of vocal flexibility.

Acknowledgments:

We would like to thank the French Ministère de l'Enseignement Supérieur et de la Recherche (PhD grant to SK), the Université de Saint-Etienne (research sabbaticals to FL and NM, visiting professorship to KZ and research funding), the European Research Council (KZ grant PRILANG 283871), Institut universitaire de France (NM), and the Labex CeLyA. We warmly thank Colette Bouchut and Nicolas Boyer for their endless support, Roger Mundry for the pDFA method, and the zoological parks of Apenheul, Planckendael and La Vallée des Singes for their welcome, and especially to the bonobo keepers for their support and patience. Lastly, we thank the two anonymous reviewers who have accepted to review this paper and have contributed to improve it.

REFERENCES

614 Aubin, T. & Jouventin, P. (2002). How to identify vocally a kin in a crowd? The
615 penguin model. *Advances in the Study of Behavior, 31*, 243-277. doi:
616 10.1016/S0065-3454(02)80010-9
617
618 Bermejo, M. & Omedes, A. (1999). Preliminary vocal repertoire and vocal
619 communication of wild bonobos (*Pan paniscus*) at Lilungu (Democratic Republic
620 of Congo). *Folia Primatologica, 70*, 328-357. doi:10.1159/000021717
621
622 Bouchet, H., Blois-Heulin, C., Pellier, A., Zuberbuhler, K. & Lemasson, A.
623 (2012). Acoustic variability and individual distinctiveness in the vocal repertoire
624 of red-capped mangabeys (*Cercocebus torquatus*). *Journal of Comparative*
625 *Psychology*, *126*, 45-56. doi:10.1037/a0025018
626
627 Bradbury, J.W. & Vehrencamp, S.L. (1998). *Principles of Animal*
628 *Communication*. New York: Sinauer Associates.
629
630 Briefer, E. F. (2012). Vocal expression of emotions in mammals: mechanisms
631 of production and evidence. *Journal of Zoology*, *288*(1), 1-20.
632
633 Briefer, E. F. (2020). Coding for 'Dynamic'Information: Vocal Expression of
634 Emotional Arousal and Valence in Non-human Animals. In N. Mathevon & T.
635 Aubin (Eds), *Coding Strategies in Vertebrate Acoustic Communication* (pp. 137-
636 162). Springer, Cham.

637

638 Casey, C., Charrier, I., Mathevon, N., Reichmuth, C. (2015). Rival assessment
639 among elephant seals: evidence of associative learning during male-male
640 contests. *Royal Society Open Science*, 2, 150228.
641 doi.org/10.1098/rsos.150228
642
643 Charrier, I., Jouventin, P., Mathevon, N. & Aubin, T. (2001). Individual identity
644 coding depends on call type in the South Polar skua, *Catharacta maccormicki*.
645 *Polar Biology*, *24*, 378-382. doi:10.1007/s003000100231
646
647 Charrier, I., Mathevon, N. & Jouventin, P. (2003). Vocal signature recognition of
648 mothers by fur seal pups. *Animal Behaviour*, *65*, 543-550. doi:
649 10.1006/anbe/2003.2073
650
651 Chapman, C.A. & Weary, D.M. (1990). Variability in spider monkeys'
652 vocalisations may provide basis for individual recognition. *American Journal of*
653 *Primatology, 22*, 279-284. doi:10.1002/ajp.1350220407
654
655 Charlton, B. D., Pisanski, K., Raine, J., & Reby, D. (2020). Coding of Static
656 Information in Terrestrial Mammal Vocal Signals. In N. Mathevon & T. Aubin
657 (Eds), *Coding Strategies in Vertebrate Acoustic Communication* (pp. 115-136).
658 Springer, Cham.
659

660 Cheney, D. L. & Seyfarth, R. M. (2018). Flexible usage and social function in
661 primate vocalisations. *Proceedings of the National Academy of Sciences,115,*
662 1974–1979. doi: 10.1073/pnas.1717572115
663
664 Clay, Z. & Zuberbuhler, K. (2009). Food-associated calling sequences in
665 bonobos. *Animal Behaviour, 77*, 1387-1396.
666 doi:10.1016/j.anbehav.2009.02.016
667
668 Clay, Z. & Zuberbuhler, K. (2011a). Bonobos extract meaning from call
669 sequences. *PLOS One, 6*, e18786. doi:10.1371/journal.pone.0018786
670
671 Clay, Z., & Zuberbuehler, K. (2011b). The Structure of bonobo copulation calls
672 during reproductive and non-reproductive sex. *Ethology, 117*, 1158-1169. doi:
673 10.1111/j.1439-0310.2011.01975.
674 Clay, Z., Archbold, J. & Zuberbuhler, K. (2015). Functional flexibility in wild
675 bonobo vocal behaviour. *PeerJ, 3*, e1124. doi: 10.7717/peerj.1124
676
677 Crockford, C. (2019). Why does the chimpanzee vocal repertoire remain
678 poorly understood?-and what can be done about it. In *The chimpanzees of the*
679 *Taï forest: 40 years of research* (pp. 394-409). Cambridge University Press.
680

681 Dentressangle, F., Aubin, T, & Mathevon, N (2012). Males use time whereas
682 females prefer harmony: individual call recognition in the dimorphic blue-footed
683 booby. *Animal Behaviour*, *84*, 413-420. doi: 10.1016/j.anbehav/2012/05/012
684
685 de Waal, F.B.M. (1988). The communicative repertoire of captive bonobos (*Pan*
686 *paniscus*) compared to that of chimpanzees. *Behaviour, 106*, 183-251. doi:
687 10.1163/156853988X00269
688
689 Elie, J.E. & Theunissen, F.E. (2018). Zebra finches identify individuals using
690 vocal signatures unique to each call type. *Nature Communications, 9*, 4026.
691
692 Ey, E. & Fischer, J. (2009). The “acoustic adaptation hypothesis” – A review of
693 the evidence from birds, anurans and mammals. *Bioacoustics, 19*, 21-48.
694
695 Fedurek, P., Zuberbühler, K., & Dahl, C. D. (2016). Sequential information in a
696 great ape utterance. *Scientific Reports, 6*, 38226.
697
698 Fischer, J., Wadewitz, P., & Hammerschmidt, K. (2017). Structural variability
699 and communicative complexity in acoustic communication. *Animal Behaviour*,
700 *134*, 229-237.
701
702 Furuchi, T. (2011). Female contributions to the peaceful nature of bonobo
703 society. *Evolutionary Anthrophology, 20*, 131-142. doi: 10.1002/evan.20308

Gersick, A.S., Cheney, D.L., Schneider, J.M., Seyfarth, R.M., & Holekamp, K.E. (2015). Long-distance communication facilitates cooperation among wild spotted hyaenas, *Crocuta crocuta. Animal Behaviour, 103*, 107-116.

Gros-Louis, J. (2004). The function of food-associated calls in white-faced capuchin monkeys, *Cebus capucinus*, from the perspective of the signaller. *Animal Behaviour*, 67(3), 431-440.

Hammerschmidt, K., & Fischer, J. (1998). The vocal repertoire of Barbary macaques: a quantitative analysis of a graded signal system. *Ethology*, *104*, 203-216.

Heinrich, B., & Marzluff, J. M. (1991). Do common ravens yell because they want to attract others? *Behavioral Ecology and Sociobiology*, 28(1), 13-21.

Hohmann, G. & Fruth, B. (1994). Structure and use of distance calls in wild bonobos (*Pan paniscus*). *International Journal of Primatology 15*, 767–782. doi:10.1007/BF02737430

Hohmann, G., & Fruth, B. (1995). Loud calls in great apes: sex differences and social correlates. In: E. Zimmermann (Ed.), *Current Topics in Primate Vocal Communication* (pp.161–184). New York, New York: Plenum Press.

727

728 Hohmann, G. & Fruth, B. (2002). Dynamics is social organization of bonobos
729 (*Pan paniscus*). In: Boesch, C., Hohmann, G. & Marchant, L.F. (Eds.),
730 *Behavioural Diversity in Chimpanzees and Bonobos* (pp.138-150). Cambridge,
731 U.K.: Cambridge University Press.

732

733 Insley, S. J. (2000). Long-term vocal recognition in the northern fur seal. *Nature*,
734 *406*, 404–5. doi:10.1038/35019064

735

736 Jansen, D.A., Cant, M.A. & Manser, M.B. (2012). Segmental concatenation of
737 individual signatures and context cues in banded mongoose (*Mungos mungo*)
738 close calls. *BMC Biology 10*, 97. doi:10.1186/1741-7007-10-97

739

740 Keenan, S., Lemasson, A., Zuberbühler, K. (2013). Graded or discrete? A
741 quantitative analysis of Campbell's monkey alarm calls. *Animal Behaviour, 85*,
742 109–118.

743

744 Keenan, S., Mathevon, N., Stevens, J.M.G., Guery, J.P., Zuberbuhler, K. &
745 Levrero, F. (2016). Enduring voice recognition in bonobos. *Scientific Reports,*
746 *6*, 22046. doi: 10.1038/srep22046.

747

748 Knörnschild, M., and Von Helversen, O. (2008). "Nonmutual vocal mother- pup
749 recognition in the greater sac-winged bat," *Animal Behaviour*, 76, 1001-1009.
750 https://doi.org/10.1016/j.anbehav.2008.05.018
751
752 Kondo, N. & Watanabe, S. (2009). Contact calls: information and social
753 function. *Japanese Psychological Research, 51*, 197–208.
754
755 Kondo, N., Izawa, E., & Watanabe, S. (2010). Perceptual mechanism for vocal
756 individual recognition in jungle crows (*Corvus macrorhynchos*): contact call
757 signature and discrimination. *Behaviour*, *147*, 1051–1072.
758 doi:10.1163/000579510X505427
759
760 Kreiman, J. & Sidtis, D. (2011). *Foundations of Voice Studies: An*
761 *Interdisciplinary Approach to Voice Production and Perception*. Blackwell
762 Publishing, Oxford, UK.
763
764 Lavan, N., Burton, A.M., Scott, S.K. & McGettigan, C. (2019). Flexible voices:
765 identity perception from variable vocal signals. *Psychonomic Bulletin &*
766 *Review, 26,* 90–102. doi:10.3758/s13423-018-1497-7
767
768 Leliveld, L.M.C., Scheumann, M. & Zimmermann, E. (2011). Acoustic correlates
769 of individuality in the vocal repertoire of a nocturnal primate (*Microcebus*

770 *murinus*). *The Journal of the Acoustical Society of America, 129*, 2278-2288.
771 doi:10.1121/1.3559680
772
773 Lemasson, A. & Hausberger, M. (2011). Acoustic variability and social
774 significance of calls in female Campbell's monkeys (*Cercopithecus campbelli*
775 *campbelli*). *The Journal of the Acoustical Society of America, 129*, 3341-3352.
776 doi:10.1121/1.3569704s
777
778 Levréro, F. & Mathevon, N. (2013). Vocal signature in wild infant chimpanzees.
779 *American Journal of Primatology, 75*, 324-332. doi:10.1002/ajp.22108
780
781 Manser, M. B., Jansen, D. A., Graw, B., Hollén, L. I., Bousquet, C. A., Furrer,
782 R. D., & Le Roux, A. (2014). Vocal complexity in meerkats and other
783 mongoose species. In: *Advances in the Study of Behavior, Vol. 46* (pp. 281-
784 310). Academic Press.
785
786 Marler, P. (1977). The structure of animal communication sounds. In: T.H.
787 Bullock (Ed.), *Recognition of complex acoustic signals*. (pp. 17–35). Berlin:
788 Springer.
789
790 Mathevon, N., Koralek, A., Weldele, M., Glickman, S.E. & Theunissen, F.E.
791 (2010). What the hyena's laugh tells us: sex, age dominance and individual

792 signature in the giggling call of *Crocuta crocuta*. *BMC Ecology, 10*.
793 doi:10.1186/1472-6785-10-9
794
795 Matrosova, V.A., Blumstein, D.T., Volodin, I.A. & Volodina, E.V. (2011). The
796 potential to encode sex, age, and individual identity in the alarm calls of three
797 species of Marmotinae. *Naturwissenschaften, 98*, 181–192.
798 doi:10.1007/s00114-010-0757-9
799
800 Maynard-Smith, J. & Harper, D. (2003). *Animal Signals.* New York: Oxford
801 University Press.
802
803 Mitani, J. C., & Nishida, T. (1993). Contexts and social correlates of long-
804 distance calling by male chimpanzees. *Animal Behaviour*, *45*(4), 735-746.
805
806 Mitani, J. C., Gros-Louis, J., & Macedonia, J. M. (1996). Selection for acoustic
807 individuality within the vocal repertoire of wild chimpanzees. *International*
808 *Journal of Primatology*, *17*, 569–583. doi:10.1007/BF02735192
809
810 Mitani, J. C., & Stuht, J. (1998). The evolution of nonhuman primate loud calls :
811 acoustic adaptation for long-distance transmission. *Primates, 39*, 171–182.
812

813 Morton, E.S. (1977). On the occurrence and significance of motivation-
814 structural rules in some bird and mammal sounds. *American Naturalist*, 111,
815 855–869.
816
817 Mundry R. & Sommer C. (2007). Discriminant function analysis with
818 nonindependent data: consequences and an alternative. *Animal Behaviour, 74*,
819 965-976. doi:10.1016/j.anbehav.2006.12.028
820
821 Pisanski, K., Nowak, J., & Sorokowski, P. (2016a). Individual differences in
822 cortisol stress response predict increases in voice pitch during exam stress.
823 *Physiology & Behavior, 163*, 234e238. doi: 10.1016/j.physbeh.2016.05.018
824
825 Pisanski, K, Cartei, V., McGettigan, C., Raine, J, & Reby, D. (2016b). Voice
826 Modulation: A Window into the Origins of Human Vocal Control? *Trends in*
827 *Cognitive Sciences, 20*, 304-318. doi:10.1016/j.tics.2016.01.002
828
829 Pisanski, K., Raine, J., & Reby, D. (2020). Individual differences in human
830 voice pitch are preserved from speech to screams, roars and pain cries. *Royal*
831 *Society open science*, *7*(2), 191642.
832
833 Price, T., Arnold, K., Zuberbuhler, K. & Semple, S. (2009). Pyow but not hack
834 calls of the male putty-nosed monkey (*Cercopithcus nictitans*) convey

information about caller identity. *Behaviour, 146*, 871-888. doi:10.1163/156853908X396610

Proops, L., McComb, K. & Reby, D. (2012). Cross-modal individual recognition in domestic horses (*Equus caballus*). *Proceedings of the National Academy of Sciences, 106*, 947-951. doi: 10.1073/pnas.0809127105

Raine, J., Pisanski, K., & Reby, D. (2017). Tennis grunts communicate acoustic cues to sex and contest outcome. *Animal Behaviour*, *130*, 47-55.

Rendall, D., Rodman, P. S. & Emond, R. E. (1996). Vocal recognition of individuals and kin in free-ranging rhesus monkeys. *Animal Behaviour, 51*, 1007-1015.

Rendall, D., Owren, M. J., & Rodman, P. S. (1998). The role of vocal tract filtering in identity cueing in rhesus monkey (Macaca mulatta) vocalisations. *Journal of Acoustic Society of American*, *103*(1), 602–614.

Robbins, M. M., Bermejo, M., Cipolletta, C., Magliocca, F., Parnell, R.J. & Stokes, E. (2004). Social structure and life-history patterns in western gorillas (*Gorilla gorilla gorilla*), *American Journal of Primatology, 64*, 145-159. doi:10.1002/ajp.20069

858 Robisson, P., Aubin, T. & Bremond, J. C. (1993). Individuality in the voice of the
859 emperor penguin, *Aptenodytes forsteri*: Adaptation to a noisy environment.
860 *Ethology*, *94*, 279-290. doi:10.1111/j.1439-0310.1993.tb00445.x
861
862 Rubow, J., Cherry, M. I., & Sharpe, L. L. (2017). A comparison of individual
863 distinctiveness in three vocalisations of the dwarf mongoose (*Helogale parvula*).
864 *Ethology*, *124*, 45–53. https://doi.org/10.1111/eth.12698
865
866 Salmi, R., Hammerschmidt, K. & Doran-Sheehy, D.M. (2014). Individual
867 distinctiveness in call types of wild western female gorillas. *PLOS One, 9*,
868 e101940. doi:10.1371/journal.pone.0101940
869
870 Schamberg, I., Cheney, D. L., Clay, Z., Hohmann, G., & Seyfarth, R. M.
871 (2016). Call combinations, vocal exchanges and interparty movement in wild
872 bonobos. *Animal Behaviour*, *122*, 109-116.
873
874 Schamberg, I., Cheney, D. L., Clay, Z., Hohmann, G., & Seyfarth, R. M.
875 (2017). Bonobos use call combinations to facilitate inter-party travel
876 recruitment. *Behavioral ecology and sociobiology*, *71*(4), 75.
877
878 Searcy, W. A., Anderson, R. C., & Nowicki, S. (2006). Bird song as a signal of
879 aggressive intent. *Behavioral Ecology and Sociobiology*, *60*, 234-241.
880

881 Silk, J. B. (2002). Grunts, girneys, and good intentions: The origins of strategic
882 commitment in nonhuman primates. *Evolution and the capacity for*
883 *commitment*, *3*, 138-157.
884
885 Snowdon, C.T & M. Hausberger (1997). *Social influences on vocal*
886 *development*. Cambridge, U.K.: Cambridge University Press.
887
888 Soltis, J., Leong, K., & Savage, A. (2005). African elephant vocal communication
889 II: Rumble variation reflects the individual identity and emotional state of callers.
890 *Animal Behaviour*, *70*, 589–599. doi:10.1016/j.anbehav.2004.11.016
891
892 Surbeck, M. & Hohmann, G. (2013). Intersexual dominance relationships and
893 the influence of leverage on the outcome of conflicts in wild bonobos (*Pan*
894 *paniscus*). *Behavioral Ecology and Sociobiology, 67,* 1767–1780. doi:
895 10.1007/s00265-013-1584-8
896
897 Taylor, A. M., Charlton, B. D., & Reby, D. (2016). Vocal production by
898 terrestrial mammals: Source, filter, and function. In: R. A. Suthers, W. T. Fitch,
899 R. R. Fay, & A. N. Popper (Eds.), *Vertebrate sound production and acoustic*
900 *communication* (pp. 229e259). New York, NY: Springer International
901 Publishing. doi: 10.1007/978-3-319-27721-9_8.
902

903 Tallet, C., Linhart, P., Policht, R., Hammerschmidt, K., Šimeček, P., Kratinova,
904 P., & Špinka, M. (2013). Encoding of situations in the vocal repertoire of piglets
905 (*Sus scrofa*): a comparison of discrete and graded classifications, *PLOS One*,
906 *8*, e71841.
907
908 Vannoni, E. & McElligott, A. G. (2007). Individual acoustic variation in fallow deer
909 (*Dama dama)* common and harsh groans: A source-filter theory perspective.
910 *Ethology*, *113*, 223–234. doi:10.1111/j.1439-0310.2006.01323.x
911
912 Vignal, C., Mathevon, N., & Mottin, S. (2004). Audience drives male songbird
913 response to partner's voice. *Nature*, *430*, 448-451.
914
915 Voigt-Heucke, S. L., Taborsky, M. & Dechmann, D.K.N. (2010). A dual function
916 of echolocation: bats use echolocation calls to identify familiar and unfamiliar
917 individuals. *Animal Behaviour*, *80*, 59–67. doi:10.1016/j.anbehav.2010.03.025
918
919 White, F. J. (1996). Comparative socio-ecology of *Pan paniscus*. In W.C.
920 McGrew, L.F. Marchant & T. Nishida (Eds.), *Great Ape Societies* (pp. 29–41).
921 Cambridge, U.K.: Cambridge University Press.
922
923 White, F. J., Waller, M., Boose, K., Merrill, M.Y. & Wood, K.D. (2015). Function
924 of loud calls in wild bonobos. *Journal of Anthropological Sciences, 93*, 1-13.
925 doi:10.4436/JASS.93003

Wiley, R. H. (2013). Specificity and multiplicity in the recognition of individuals: implications for the evolution of social behaviour. *Biological Reviews*, *88*, 179–195.

933 Table 1. Automatic and manual acoustic parameters
934
935

Acoustic parameters	Description/Calculation
F_0-Start	Fundamental frequency at beginning of the call (Hz)
F_0-End	Fundamental frequency at end of the call (Hz)
F_0-Peak	Highest frequency reached on the fundamental (in Hz)
F_0-Peak Time	Point over the duration of the call at which F_0-Peak is reached. Manually calculated as a proportion: time of F_0-Peak(s) / Call Duration (s)
Call Duration	Length of call (s)
Ascending Slope	Calculated as: (F_0-Peak – F_0-Start) / (F_0-Peak Time – 0)
Descending Slope	Calculated as: (F_0-End – F_0-Peak) / (1 – F_0Peak Time)
Slope– F_0 Start to Mid	Calculated as: (F_0 at midpoint of call duration – F_0-Start) / (Time at midpoint of call duration – 0)
Slope– F_0 Mid to End	Calculated as: (F_0-End – F_0 at midpoint of call duration) / (Call duration – Time at midpoint of call duration)
Q25 Frequency	**The frequency at which the call is divided into two intervals, the first quartile contains 25% of the call's energy (Hz)**
Q25 Time	**The time at which the call is divided into two intervals, the first quartile contains 25% of the call's energy (s)**

Q50 Frequency	**The median - the frequency at which the call is divided into two frequency intervals of equal energy (Hz)**
Q75 Frequency	**The third quartile – contains 75% of the call's energy (Hz)**
Q75 Time	**The third quartile – contains 75% of the call's energy (s)**
Maximum Frequency	**The frequency at which the maximum energy occurs in the call (Hz)**
Maximum Time	**The first time point along the call where maximum amplitude occurs on waveform (s)**

936

937 Non-bold text are the manually measured or calculated measurements, and
938 bold text are automatically calculated by the Raven program.

939

Table 2. Call type usage in each context

	Percentage of calls given in each context				
Contexts	High-hoot	Bark	Soft Bark	Peep-yelp	Peep
Aggression	**23.12**	**19.03**	2.66	0.00	0.00
Change in environment	18.02	13.46	9.93	2.86	1.58
External Event (Alarm)	13.81	6.96	2.18	2.14	0.79
Pre-feeding	**38.74**	**34.34**	**21.55**	17.38	21.74
Feeding	1.80	18.10	**38.26**	**36.19**	**28.46**
Forage	4.50	3.25	18.40	15.95	9.09
Groom	0.00	0.93	1.45	6.43	9.88
Contact-general	0.00	3.94	5.57	**19.05**	**28.46**

The two contexts in which each call type is most commonly used are in bold. (Percentages presented for clarity only; chi-square results were generated by analysing observed vs. expected values of call rates.)

947 Table 3. Potential for individual coding (PIC)
948
949

		PIC values by Call Types				
Individual Parameters	Overall PIC value for each parameter	Peep	Peep -yelp	Soft bark	Bark	High-hoot
F_0-Start	1.20	**1.23**	1.24	1.12	**1.29**	1.38
F_0-End	1.11	1.20	1.18	**1.20**	1.19	1.43
F_0-Peak	1.20	1.21	**1.25**	1.12	1.25	**1.46**
F_0-Peak Time	1.08	0.91	1.03	1.04	1.06	1.18
Call Duration	1.16	1.05	1.13	**1.20**	1.19	1.28
Ascending Slope	**1.22**	0.97	1.15	1.06	1.19	1.14
Descending Slope	1.03	1.06	1.17	1.08	1.02	1.21
Q25 Frequency	1.17	1.17	1.11	1.12	1.17	1.38
Q25 Time	1.07	0.99	1.01	1.03	1.15	1.06
Q50 Frequency	1.12	1.15	1.11	1.10	1.22	1.36
Q75 Frequency	1.14	1.17	1.08	1.18	1.23	1.34
Q75 Time	1.09	1.00	1.05	1.06	1.12	1.14
Maximum Frequency	1.08	1.12	1.08	1.08	1.11	1.28
Maximum Time	1.10	1.02	1.03	1.03	1.10	1.08
Overall PIC for call type		1.03	1.10	1.08	1.18	1.22

950

951 Investigation of the potential for individuality in each call type as well as each
952 parameter across all call types and within each call type separately. A PIC
953 greater than or equal to 1 suggests potential for individuality. For each call type,
954 the parameter with the highest PIC is in bold.
955

956 Figure 1. Acoustic and temporal measurements. Example of manual
957 measurements taken on a soft bark call: a= F0-Start, b=F0-Midpoint (not
958 included in analysis but used to calculate other measurements), c=F_0-Peak, d=
959 F_0-End. Call duration=time at b) – time at a).
960
961
962 Figure 2. Spectrographic illustrations of the five most common call types of the
963 bonobo repertoire. Spectrogram images depict: 1) High-hoot; 2) Bark; 3) Soft
964 bark; 4) Peep-yelp; 5) Peep. Panel 6) shows the confusion matrix obtained from
965 the permuted DFA classifying the five call types, which are labelled as just listed.
966 The classification rate was of 60% for High-hoot, 44% for Bark, 48% for Soft
967 bark, 58% for Peep-yelp and 62% for Peep. On the confusion matrix, the
968 diagonal shows the rate at which a call type was correctly assigned –
969 specifically, what percentage the actual call type and the predicted call type
970 match. The brightness of each diagonal yellow square corresponds to the
971 strength of classification. The off-diagonal cells show percentage of
972 misclassification for each call type and which other call type they were
973 misclassified as.
974
975
976 Figure 3. Acoustic gradation and individual signature coding in the bonobo vocal
977 repertoire. Top: The scatterplot illustrates the graded nature of the acoustic
978 properties of the five call types. The Table displays the factor loadings on

Discriminant function 1 and 2. White asterisks mark the centroid of each call type. Bottom graph: The mean percentage of correct classification for individual identity is reported for each call type, illustrating that the reliability of the vocal signature increases from peeps to high-hoots.

Figure 4. Individual vocal signatures in five different call types. 1) High-hoots (mean correction classification rate: 53%); 2) Barks (mean correction classification rate: 44%; 3) Soft Barks (mean correction classification rate: 30%); 4) Peep-yelps (mean correction classification rate: 30%); 5) Peeps (mean correction classification rate: 23%). Each confusion matrix shows the results of five separate permuted DFAs investigating the strength individuality in each call type. The confusion matrix shows the probability that an individual's calls were correctly classified after 100 iterations – the legend shows the percent accuracy for each individual (the accurate percentages are given in Supplementary Table A4; Random classification at 10%). Details on each individual, age, sex, rank, zoo and number call contributed to each analysis can be found in Supplemental Table A1.)

SUPPLEMENTAL TABLES

Supplemental Table A1. Group composition and numbers of calls contributed per individual

Name (Abbr)	Sex	Age	Rank	Zoo	Bark	High-hoot	Peep	Peep-yelp	Soft bark
Hortense (Ho)	F	35	High	Apen	*15	✓*18	✓*32	✓*15	11
Jill (Ji)	F	28	High	Apen	*55	✓*52	✓*25	*51	✓*44
Zuani (Zu)	F	23	High	Apen	✓*26	✓*45	0	*15	*26
Bolombo (Bo)	M	16	Low	Apen	✓*37	0	✓*25	✓*29	✓*15
Zamba (Za)	M	15	Mid	Apen	✓*14	✓*48	✓*18	✓*23	*18
Kumbuka (Ku)	F	14	Mid	Apen	✓*32	✓*19	✓*27	*12	*20
Besede (N/A)	F	8	Low	Apen	N/A	N/A	N/A	N/A	N/A
Yahimba (N/A)○	F	4	N/A	Apen	N/A	N/A	N/A	N/A	N/A

Makasi○ (N/A)	M	4	N/A	Apen	N/A	N/A	N/A	N/A	N/A
Monyama (N/A)	F	3	N/A	Apen	N/A	N/A	N/A	N/A	N/A
Lina (Li)	F	28	High	Planc	✓*17	2	6	✓*21	✓*28
Vifijo (Vi)	M	19	Low	Planc	✓*27	0	✓*14	✓*19	6
Djanoa (Dj)	F	18	Mid	Planc	6	11	5	✓*23	✓*32
Louisoko (Ls)	M	15	Mid	Planc	✓*32	6	3	10	✓*26
Lucuma (Lc)	M	11	Mid	Planc	*13	0	3	*15	✓*14
Busira (N/A)○	F	10	Low	Planc	N/A	N/A	N/A	N/A	N/A
Habari (N/A)○	M	7	Low	Planc	N/A	N/A	N/A	N/A	N/A
Lingoye (N/A)○	F	8	Mid	Planc	N/A	N/A	N/A	N/A	N/A
Nayoki (N/A)	F	2	N/A	Planc	N/A	N/A	N/A	N/A	N/A
Daniela	F	45	High	VDS	1	0	✓*14	✓*38	*35

(Dd)									
Lisala (Lsl)	F	33	Mid	VDS	2	4	3	7	✓*35
Ukela (Uk)	F	28	High	VDS	*14	✓*18	1	10	✓*19
Bondo (N/A)○	M	22	Low	VDS	N/A	N/A	N/A	N/A	N/A
Kirembo (Kir)	M	21	Low	VDS	2	2	✓*22	✓*15	8
Ulindi (Ul)	F	20	Mid	VDS	*24	✓*17	8	✓*16	*14
David (Dv)	M	12	Mid	VDS	5	9	✓*15	*29	✓*19
Diwani (Dw)	M	17	Mid	VDS	✓*50	✓*23	5	9	8
Khaya (Kh)	F	12	Mid	VDS	✓*24	✓*17	8	*17	6
Lucy (Ly)	F	10	Low	VDS	✓*22	✓*30	✓*13	*17	7
Lingala (Lng)	F	10	Mid	VDS	*13	*12	6	✓*29	✓*22
Kelele (N/A)	M	9	Low	VDS	N/A	N/A	N/A	N/A	N/A

Luebo (N/A)○	M	6	N/A	VDS	N/A	N/A	N/A	N/A	N/A
Nakala (N/A)○	F	5	N/A	VDS	N/A	N/A	N/A	N/A	N/A
Loto (N/A)○	M	4	N/A	VDS	N/A	N/A	N/A	N/A	N/A
Khalessi (N/A)○	F	1	N/A	VDS	N/A	N/A	N/A	N/A	N/A
Moko (N/A)○	M	1	N/A	VDS	N/A	N/A	N/A	N/A	N/A

✓Indicates individuals included in pDFA analysis**.** *Indicates individual included in PIC and variability analysis. ○Indicates individuals who were not included in the study, which was all individuals under the age of 10 and an adult male and female both with low calling rates.

1011 Supplemental Table A2. Acoustic description of each call type

1012

		Call Types				
Acoustic parameters		High-hoot N=333	Bark N=431	Soft Bark N=413	Peep-Yelp N=420	Peep N=253
F_0-Start	MEAN	1031.73	1352.51	1543.31	1364.85	1342.38
	S.D.	*490.48*	*586.69*	*340.01*	*357.09*	*376.35*
F_0-End	MEAN	1285.32	1420.46	1405.03	1363.51	1354.77
	S.D.	*404.58*	*423.75*	*393.69*	*375.72*	*384.72*
F_0-Peak	MEAN	2392.79	2219.37	1928.1	1607.05	1401.18
	S.D.	*332.98*	*365.34*	*286.36*	*331.53*	*382.08*
F_0-Peak Time	MEAN	0.468	0.443	0.45	0.512	0.308
	S.D.	*0.131*	*0.123*	*0.149*	*0.202*	*0.36*
Call Duration	MEAN	0.239	0.193	0.172	0.158	0.106
	S.D.	*0.067*	*0.057*	*0.048*	*0.044*	*0.038*
Ascending	MEAN	3236.07	1978.76	858.14	479.93	101.31
Slope	*S.D.*	*1968.15*	*1200.45*	*564.47*	*391.53*	*147.78*
Descending	MEAN	-2083.48	-1464.78	-953.52	-510.31	-78.25
Slope	*S.D.*	*847.28*	*782.78*	*630.38*	*494.19*	*114*
Slope- F_0Start	MEAN	11124.01	8787.26	4146.4	2821.28	654.03
to Mid	*S.D.*	*5093.9*	*5819.3*	*3021.21*	*2310.53*	*1583.44*
Slope- F_0 Mid	MEAN	-8891.67	-8096	-5849.33	-2757.86	-459.76
to End	*S.D.*	*4194.48*	*4878.49*	*4131.16*	*2635.8*	*1306.48*

Q25 Frequency	MEAN	1953.65	1832.98	1796.7	1509.9	1346.47
	S.D.	*679*	*501.88*	*414.84*	*414.53*	*404.16*
Q25 Time	MEAN	0.084	0.072	0.065	0.057	0.037
	S.D.	*0.048*	*0.048*	*0.042*	*0.038*	*0.031*
Q50 Frequency	MEAN	2436.3	2155.83	2028.72	1708.41	1488.27
	S.D.	*759.6*	*592.43*	*573.09*	*571.71*	*516.4*
Q75 Frequency	MEAN	2952.44	2639.05	2354.58	2009.77	1723.85
	S.D.	*953.46*	*871.97*	*777.02*	*757.62*	*696.86*
Q75 Time	MEAN	0.171	0.136	0.118	0.106	0.072
	S.D.	*0.063*	*0.058*	*0.049*	*0.044*	*0.042*
Maximum	MEAN	2324.69	2075.19	2026.32	1743.69	1477.03
Frequency	*S.D.*	*952.46*	*742.84*	*658.31*	*674.38*	*547.96*
Maximum Time	MEAN	0.124	0.102	0.091	0.08	0.054
	S.D.	*0.075*	*0.059*	*0.046*	*0.042*	*0.029*

The mean and standard deviation (S.D.) of each acoustic parameter for each call type are given.

Supplemental Table A3. Results from post-hoc comparisons between each call type on their different contextual usage

	df	$\chi 2$	Likelihood Ratio	*N*	*p*
High-hoot – Bark	7	76.296	94.65	764	< 0.001
High-hoot – Soft Bark	7	290.838	346.057	746	< 0.001
High-hoot – Peep-yelp	7	419.855	526.550	753	< 0.001
High-hoot – Peep	7	346.154	437.113	586	< 0.001
Bark – Soft Bark	7	153.934	166.575	844	< 0.001
Bark – Peep-yelp	7	265.360	309.841	851	< 0.001
Bark – Peep	7	216.074	252.697	684	< 0.001
Soft Bark – Peep-yelp	7	73.984	82.075	833	< 0.001
Soft Bark – Peep	7	119.831	126.653	666	< 0.001
Peep-yelp – Peep	6*	21.447	21.840	673	0.002

*There were no peep-yelps or peeps given in the aggression context, therefore the df for that comparison is 6 as compared to 7 for the other comparisons.

Supplemental Table A4. Individual vocal signatures in high-hoots

	Predicted individual									
Actual individual	Dw	Ho	Ji	Kh	Ku	Ly	Uk	Ul	Za	Zu
Dw	**50**	3	11	7	1	16	1	1	9	0
Ho	2	**70**	18	0	0	0	1	3	6	0
Ji	3	9	**49**	3	1	10	16	2	1	6
Kh	1	0	9	**35**	0	17	17	10	3	7
Ku	5	0	0	3	**77**	8	0	7	0	1
Ly	12	0	6	24	6	**39**	11	0	1	0
Uk	5	2	24	12	0	4	**31**	13	0	8
Ul	0	2	3	1	7	1	17	**60**	1	8
Za	21	1	0	4	3	7	0	0	**63**	0
Zu	0	0	1	14	0	1	9	19	0	**56**

The table shows the accurate results of a permuted DFAs investigating the strength individuality in High-hoot calls. It shows the probability that an individual's calls were correctly classified (namely the number of times out of 100 iterations where the identity of the "predicted individual" by the pDFA matches with the "actual individual" identity; Random classification at 10%). The names of individuals are abbreviated in two letters, *c*orrect individual classifications are in bold. Details on each individual, age, sex, rank, zoo and

1035 number call contributed to each analysis can be found in Supplemental Table
1036 A1). The mean correct classification rate of high-hoots was 53%.
1037

1038 Supplemental Table A5. Individual vocal signatures in barks

1039

	Predicted individual									
Actual individual	Bo	Dw	Kh	Ku	Li	Ls	Ly	Vi	Za	Zu
Bo	**44**	1	9	0	14	13	3	6	8	3
Dw	4	**34**	17	4	0	2	11	12	14	2
Kh	20	10	**22**	6	3	10	9	4	0	16
Ku	4	3	5	**63**	4	5	9	5	2	0
Li	12	1	2	1	**37**	11	5	1	7	24
Ls	12	0	4	3	5	**63**	0	1	0	11
Ly	4	15	7	5	8	1	**52**	5	0	3
Vi	18	6	8	0	1	6	3	**36**	21	2
Za	2	16	4	8	1	3	1	19	**46**	0
Zu	14	0	2	4	9	21	1	4	2	**42**

1040

1041 Same legend as on the Supplemental Table A4 but for barks. The mean correct

1042 classification rate of barks was 44%.

1043

1044 Supplemental Table A6. Individual vocal signatures in soft barks

1045

	Predicted individual									
Actual individual	Bo	Dv	Dj	Ji	Li	Lng	Lsl	Ls	Lc	Uk
Bo	**26**	2	19	13	11	10	4	11	3	1
Dv	0	**36**	3	3	3	16	5	15	11	8
Dj	15	12	**16**	10	24	2	2	8	6	4
Ji	13	5	6	**26**	4	7	4	20	10	7
Li	8	7	23	10	**34**	0	2	12	3	1
Lng	7	9	3	16	0	**26**	8	8	16	7
Lsl	5	9	9	5	12	12	**16**	11	4	16
Ls	4	10	5	13	10	12	5	**23**	16	2
Lc	4	8	6	11	6	8	1	20	**34**	1
Uk	4	8	3	2	0	5	10	0	3	**66**

1046

1047 Same legend as on the Supplemental Table A4 but for soft barks. The mean
1048 correct classification rate of soft barks was 30.15%.

1049

1050 Supplemental Table A7. Individual vocal signatures in peep-yelps

1051

	Predicted individual									
Actual individual	Bo	Dd	Dj	Ho	Ki	Li	Lng	Ul	Vi	Za
Bo	**12**	8	12	2	15	25	7	5	9	4
Dd	2	**26**	4	4	11	0	9	21	17	6
Dj	12	6	**11**	5	11	29	3	4	14	5
Ho	4	6	9	**13**	3	8	6	5	32	14
Ki	11	15	19	1	**14**	10	10	9	7	4
Li	14	3	11	4	8	**36**	10	1	2	13
Lng	6	8	6	8	21	6	**30**	5	8	3
Ul	1	32	0	1	3	0	11	**40**	12	1
Vi	4	14	3	32	15	2	4	3	**18**	5
Za	5	1	10	1	3	13	1	8	4	**55**

1052

1053 Same legend as on the Supplemental Table A4 but for peep-yelps. The mean

1054 correct classification rate of peep-yelps was 25.5%.

1055

Supplemental Table A8. Individual vocal signatures in peeps

	Predicted Individual									
Actual individual	Dw	Ho	Ji	Kh	Ku	Ly	Uk	Ul	Za	Zu
Dw	**34**	1	11	15	3	0	10	10	7	10
Ho	1	**24**	20	8	5	17	5	3	16	2
Ji	11	19	**26**	17	10	3	5	3	2	5
Kh	7	8	7	**30**	4	4	8	8	9	14
Ku	9	12	8	6	**21**	5	15	11	6	7
Ly	1	9	12	1	12	**32**	6	7	15	6
Uk	14	13	3	7	21	6	**9**	12	9	7
Ul	12	11	4	13	5	6	22	**8**	7	13
Za	1	36	0	2	5	14	7	9	**21**	5
Zu	11	3	2	23	6	8	8	10	1	**27**

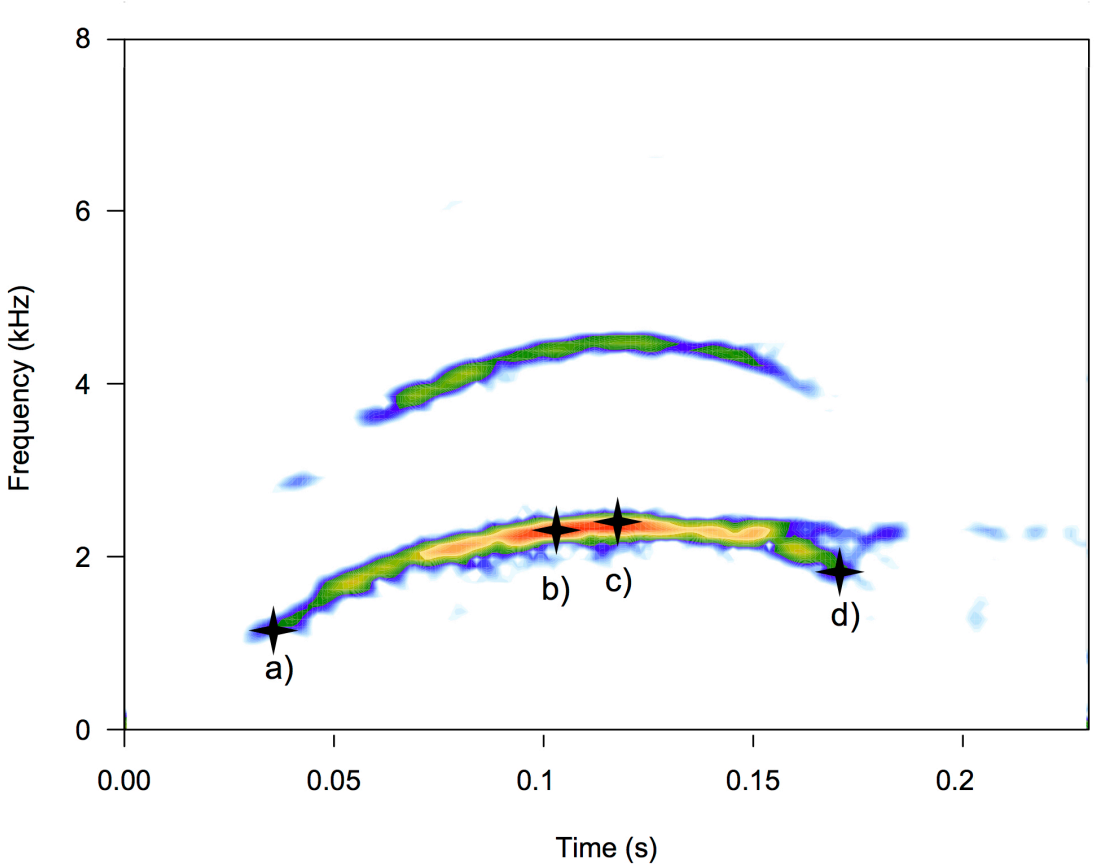
Same legend as on the Supplemental Table A4 but for peeps. The mean correct classification rate of peeps was 23.1%.

Acknowledgments:

We would like to thank the French Ministère de l'Enseignement Supérieur et de la Recherche (PhD grant to SK), the Université de Saint-Etienne (research sabbaticals to FL and NM, visiting professorship to KZ and research funding), the European Research Council (KZ grant PRILANG 283871), Institut universitaire de France (NM), and the Labex CeLyA. We warmly thank Colette Bouchut and Nicolas Boyer for their endless support, Roger Mundry for the pDFA method, and the zoological parks of Apenheul, Planckendael and La Vallée des Singes for their welcome, and especially to the bonobo keepers for their support and patience. Lastly we thank the two anonymous reviewers who have accepted to review this paper and have contributed to improve it.

Figure

1



Figure

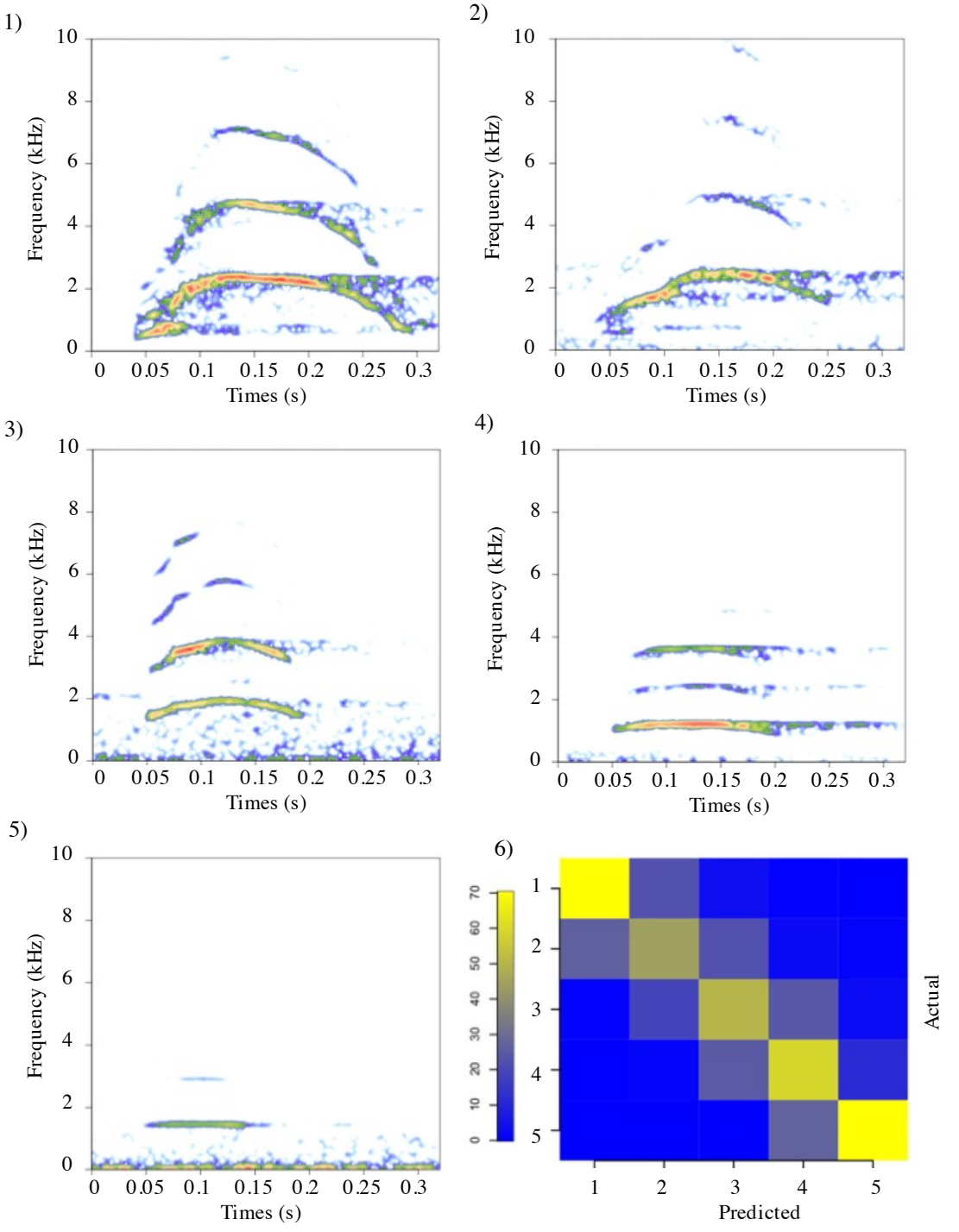
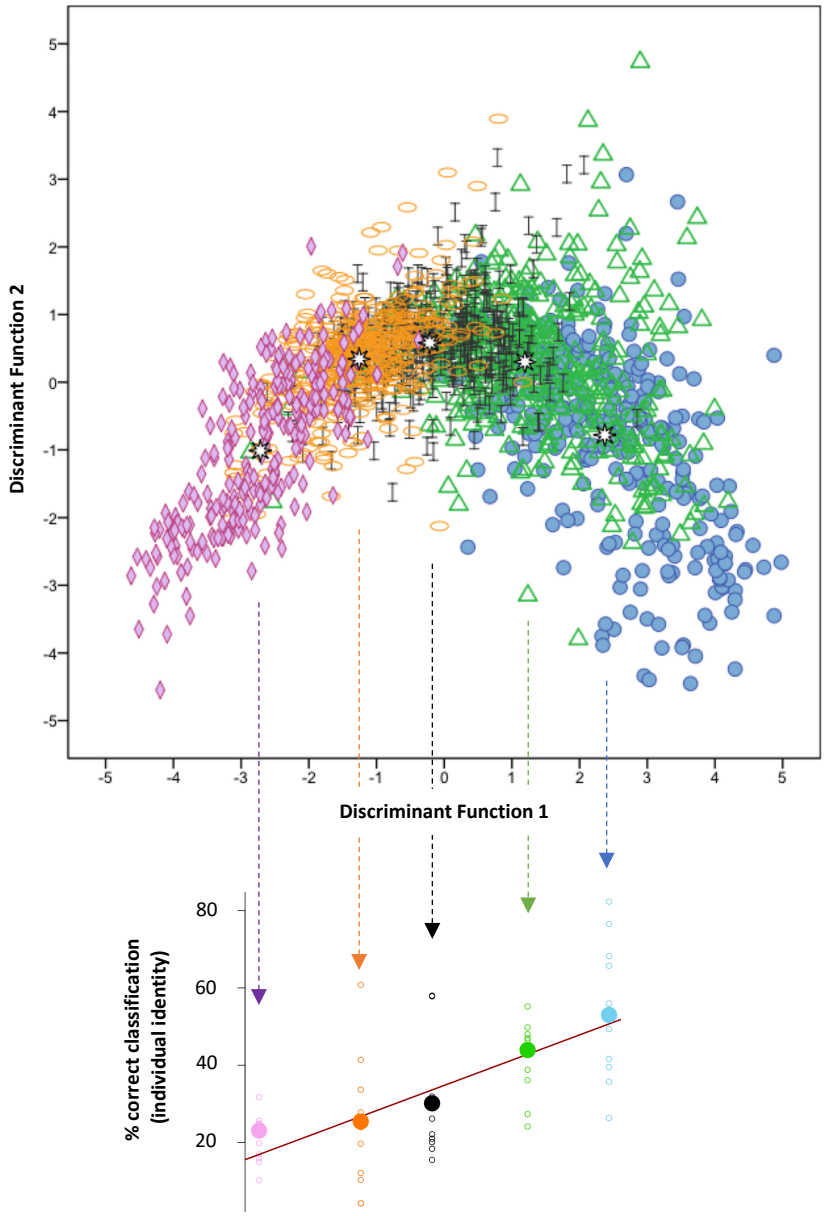


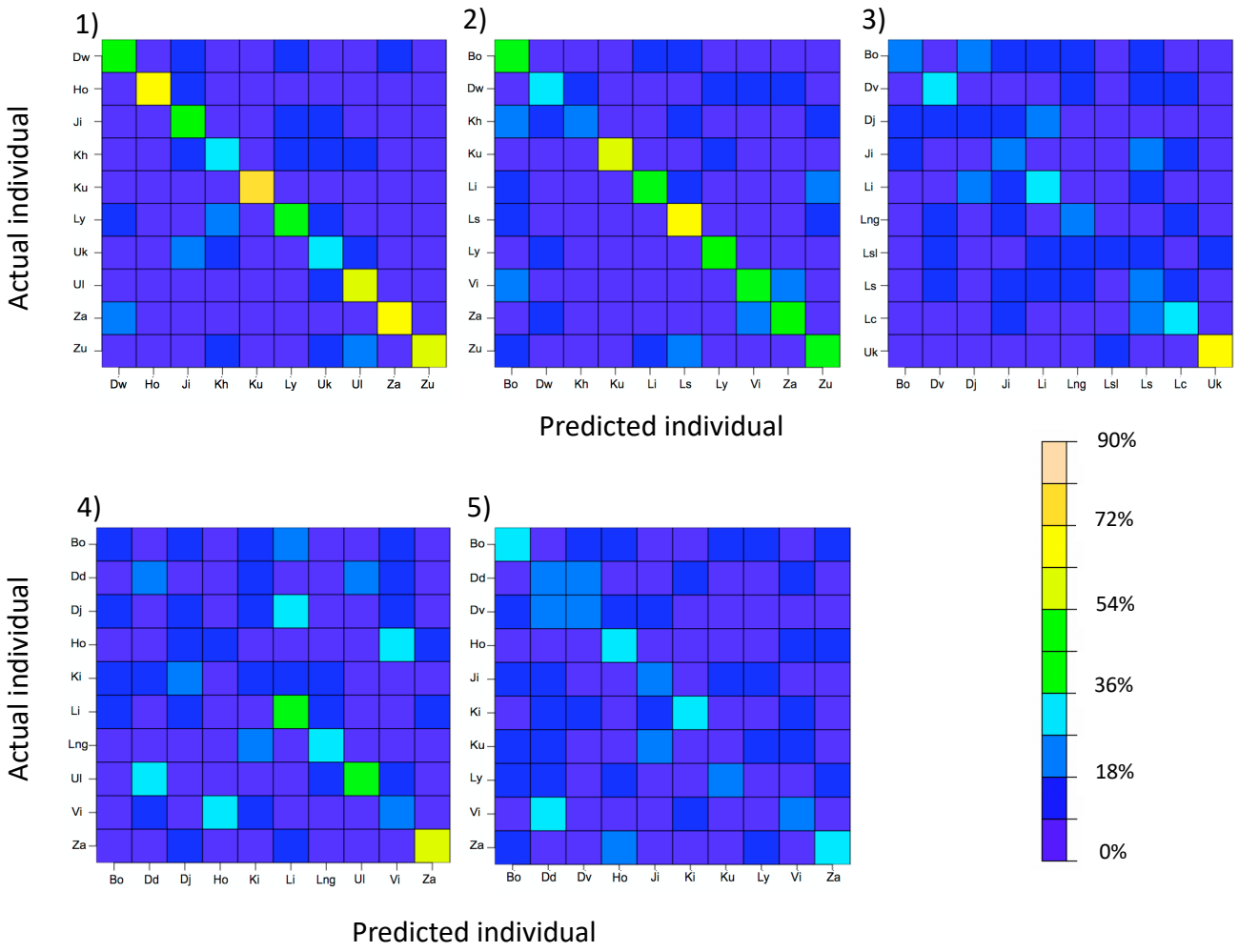
Figure 3



	Function 1	Function 2
F_0-Start	-0.121	**0.436**
F_0-End	-0.015	0.146
F_0-Maximum	**0.616**	0.024
F_0-Maximum proportion	0.076	**0.293**
Call Duration	**0.445**	-0.003
Ascending Slope	**0.59**	-0.452
Descending Slope	**-0.612**	0.151
Slope-Start to Midpoint	**0.543**	-0.183
Slope-Midpoint to End	**-0.467**	-0.166
Q1 Frequency	0.244	0.111
Q1 Time	0.195	0.068
Q3 Frequency	0.299	-0.012
Q3 Time	0.34	-0.044
Centre Frequency	0.303	0.006
Maximum Frequency	0.214	0.057
Maximum Time	0.238	0.019

Figure

4


1)
2)
3)
4)
5)
Actual individual
Predicted individual
Dw Ho Ji Kh Ku Ly Uk Ul Za Zu
Bo Dw Kh Ku Li Ls Ly Vi Za Zu
Bo Dv Dj Ji Li Lng Lsl Ls Lc Uk
Bo Dd Dj Ho Ki Li Lng Ul Vi Za
Bo Dd Dv Ho Ji Ki Ku Ly Vi Za
90%
72%
54%
36%
18%
0%

Animal Welfare Note

All research conducted for this research paper was observational and no experimental manipulations occurred. All data collection protocols were performed in accordance with the relevant guidelines and regulations, and were approved by the Institutional Animal Ethical Committee of the University of Lyon/Saint-Etienne, under the authorization no. 42-218-0901-38 SV 09 (Lab ENES).